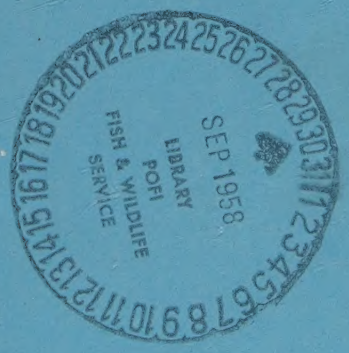
Marine Research

SCOTTISH HOME DEPARTMENT

Marine Research
1958 No. 3

Lernaeocera obtusa n.sp. Its Biology and its Effects on the Haddock

By Z. KABATA, B.Sc.



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Lernaeocera obtusa n.sp.—Its Biology and its Effects on the Haddock

INTRODUCTION

The very nature of their life makes ectoparasites more noticeable than endoparasites, hidden within eir hosts. Few of the ectoparasites have stimulated so much interest, both among the scientific observers d among the practical fishermen, as those belonging to genus *Lernaeocera*. The 'knobs' or 'buttons'— the latter call them—are frequently discussed and examined aboard the fishing vessels. They have en found to be full of blood and their harmful nature is often suspected.

There is no agreement among the many biologists who have studied *Lernaeocera* as to the extent of ury caused to its final host, the gadoid fish. However, with one exception (Mann, 1952), all these rkers were interested in *Lernaeocera* mainly as an unusual animal and concerned themselves little th its relationship with the host fish.

Among the first to give opinion on the influence of *Lernaeocera branchialis* L. were T. and A. Scott. Scott (1909) connected this parasite with an extreme degree of emaciation in the fish, but was not ite certain which came first. Was the parasite an instrument of this wasting, reducing the fish to skin d bones, or was its presence only a consequence of the poor condition of its host, which was unable repel the invasion? A. Scott (1929) was able to find infested fish in a catch by simply picking out the st emaciated individuals. But this is hardly the best method of estimating the effect of a parasite on the st, since it brings to notice only the extreme cases. How many infested but not emaciated fishes escaped ection? The question was left open.

Sproston and Hartley (1941) not only failed to find extreme emaciation among the infested whiting d pollack of the Plymouth area but, on applying the condition factor as the test of the condition of ies, found no correlation between the state of the fish and the infestation with *Lernaeocera*. Capart 48) also considered this parasite as being without commercial importance and exerting no appreciable uence on its hosts.

The most serious effort to determine the effect of *Lernaeocera* on the host fish was made by Mann 52), who examined cod, whiting and haddock and found a definite relation between the condition the fish and the infestation. The infested fishes were usually, though not invariably, diminished in ght. The average loss of weight amounted to 5-20%, depending on the species. Mann also determined t the infested fishes suffer from secondary anaemia with all its physiological consequences.

The purpose of the present work was to determine the effects of *Lernaeocera* on the haddock (*Gadus efinus* L.) and to find out as much as possible about the biology of the parasite itself, and thereby understand better its harmful potentialities. During the course of investigations it became apparent t the *Lernaeocera* infesting haddock differs from that parasitising whiting and other gadoids. The erences were of such a character and extent that they could be explained only by the existence of cific distinctions between the two types of *Lernaeocera*. Closer investigation of this problem resulted the description of a new species of *Lernaeocera* which was reported elsewhere (Kabata, 1957). This cies, *L. obtusa*, is the subject of the present paper. The paper is divided into two parts, the first dealing h the biology of the parasite, the second with its effects on the host.

To avoid confusion the term 'stage I female' has been applied in this paper to the female *Lernaeocera*, ch is sexually mature but still attached to the intermediate host. The female from the final host is rred to as 'stage II female'. When *Lernaeocera* is mentioned without the specific name being added, statement concerns both species, *L. branchialis* and *L. obtusa*.

PART ONE

Biology of *Lernaeocera obtusa*

DESCRIPTION OF THE SPECIES

Lernaeocera obtusa, which until recently has been included in the species *L. branchialis*, has escape detection for a long time for two reasons. The first was that the main efforts of the previous investigato had been concentrated in areas in which *L. obtusa* is relatively rare. Most of them studied *Lernaeoce* in the southern parts of the North Sea and the Atlantic coast of southern Europe, where haddock, th main and probably the only final host of *L. obtusa*, is less abundant or even completely missing. Th second reason was the apparently indeterminate shape of the body of the adult (stage II) female *Lernae cera* which discouraged closer investigation of its morphological characteristics. To appreciate fully th differences between *L. branchialis* and *L. obtusa* it is necessary to examine relatively large numbers each and to take as the measure of their structural dissimilarities the differences between the means various characters.

The differences between the two species have been examined in the mature males from their inte mediate hosts and in the adult females from their final hosts (Kabata, 1957). The males cannot b used for specific diagnosis, because of their general resemblance and because of the influence of th intermediate host on their size and with it the proportions of the body. The female of *L. obtusa* is also similar general shape to that of *L. branchialis*, but it can usually be distinguished *in situ* by the angle its genital flexure (Fig. 1A). Out of 65 individuals of *L. obtusa* only 21 had a genital flexure of less tha 90°, with an overall range of 61-140° and an average of 99°. The corresponding range for *L. branchia* (Fig. 1B) was 18-111°, with an average of 66°. The specific ranges for these values overlap, but th percentage of this intergradation (Ginsburg, 1938) is only 18·8% which by itself denotes a difference at least sub-specific level. Another morphological difference is the thickness of the neck in relation the thickness of the body, which is even more pronounced. The ratio of the diameters of the neck that of the body for *L. obtusa* ranges from 0·26 to 0·41, with a mean of 0·31 (for 20 individuals). Th same ratio for *L. branchialis* ranges from 0·35 to 0·66, with a mean of 0·48. The neck of *L. obtusa* is there fore much thicker than that of *L. branchialis*. The ranges overlap only to the extent of 10%, which giv this feature specific value (Ginsburg, 1938). Another and very pronounced difference is the shape of th junction of the trunk and neck area. In *L. obtusa* the neck passes into the trunk more gradually and form with it an angle of 93° average. In *L. branchialis* this angle is much more acute and in some cases the tw sectors of the body run parallel (Fig. 1B). The transition from the neck to the trunk is associated *L. branchialis* with a large and characteristic bulge which is smaller or altogether missing in *L. obtusa*.

Some of the earlier workers considered such differences in the morphology of *Lernaeocera* to be d to environmental influences and to have no diagnostic significance. In his earlier paper (1957) the prese author has argued that these morphological features can and should be taken into account in identi cation of the species. The two parasites appear to be distinct even when only their ecology is considere and the morphological features confirm this.

LIFE HISTORY

The life history of *L. obtusa* does not differ greatly from that of *L. branchialis*. Both infest a flatfish an intermediate host and a gadoid fish as a final host. The eggs are carried by the gravid female, wh attached to the final host, in long, coiled uniseriate strings, two of which are produced by every fema The eggs are produced and pass from the strings more or less continuously and upon liberation sink

e bottom, where they hatch. The larva which emerges from them is a typical nauplius, very similar ke all the remaining developmental stages) to *L. branchialis*. The nauplius, after a short period of pelagic e, sinks to the bottom and becomes, after moulting, a copepodid. Capart (1948) has observed a meta- uplius stage in *L. branchialis* and it is thought (Sproston, 1941) that this stage might be sometimes ppressed. Possibly any flat fish might be chosen to settle on (the copepodids have been observed to tle even on empty egg-strings, on which they moulted), but the parasite is found only or almost only the lemon sole *Microstomus kitt* (Walbaum), (Kabata, 1957). Its prehensile second antennae grip mly the tissues of the gill filaments and become the main anchoring device. How the larva seeks out e host is not known, but it is possible that, as at a later stage, rheotropism is involved, causing the va to move against the respiratory current and thus to enter the gill chamber. The fact that the great ajority of the larvae are attached at or near the distal points of the gill filaments seems to indicate that s supposition is correct.

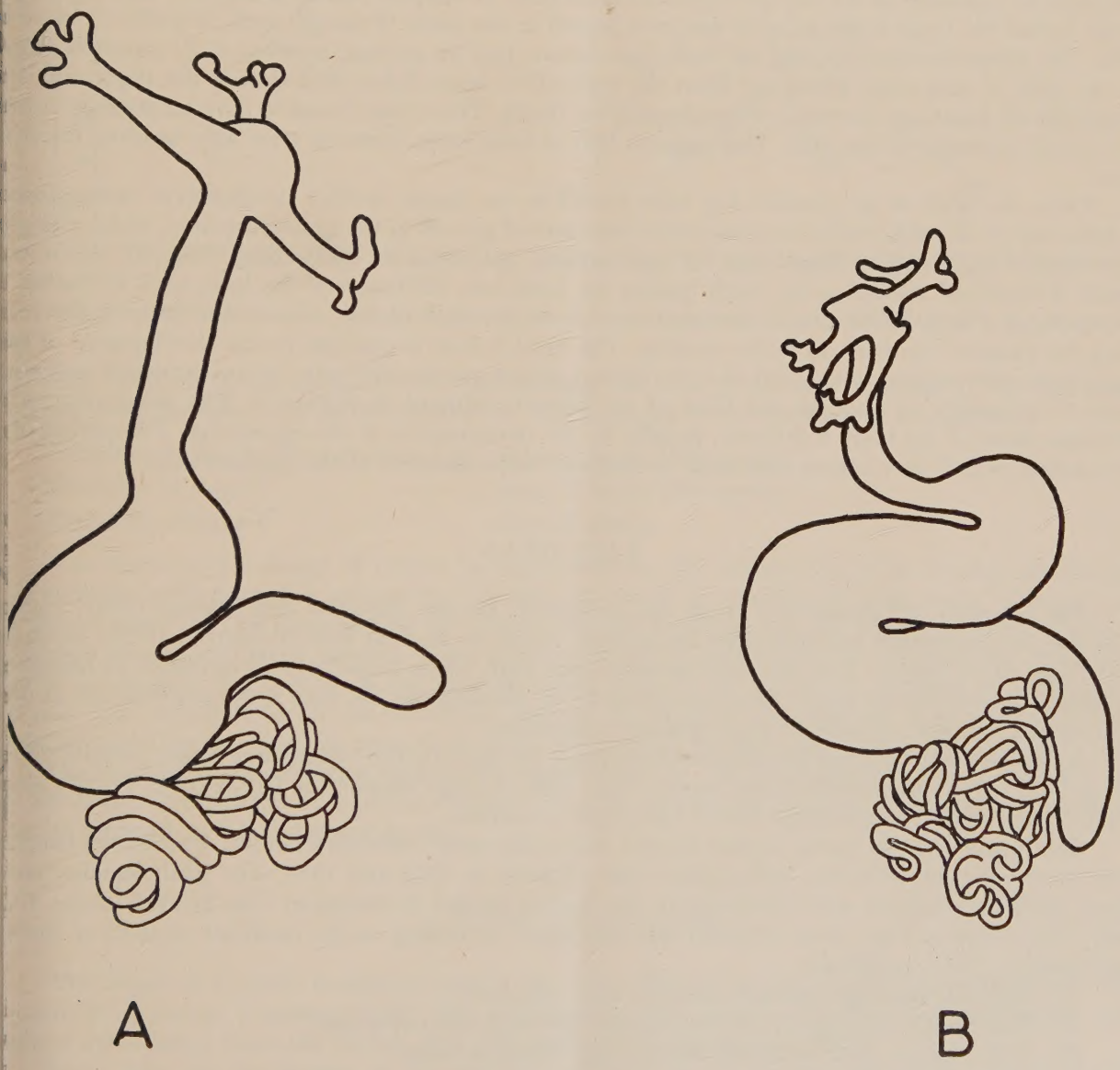

Fig. 1 Showing the differences in morphology of adult females of *L. obtusa* (A) and *L. branchialis* (B).

As in *L. branchialis*, the copepodid of *L. obtusa* passes into the first chalimus (pupal) stage a moulting and becomes attached to the gills by a double chitinous filament produced by the fro gland. The filament passes into the tissue of the gill through the punctures made in it by the chela the second antennae. The larvae then develop, by moulting several times, through three more chali stages and eventually become sexually mature males and females. At this point the male breaks off filament and seeks out the female, which it fertilises. The impregnated female separates from the and leaves the branchial chamber of the intermediate host. There follows a short period of free-swimm life, during which the parasite must find the final host, without which it cannot survive. The ma die shortly after copulation. In experiments conducted by the author in the aquarium of the Ma Laboratory, Aberdeen, it has been established that both male and female *Lernaeocera* may become attac to the final host, the attachment being effected by means of the second antennae in the same man as earlier on the intermediate host. The males do not survive long, however, and drop away from gills. The females gradually make their way along the gill filaments, the circulation of which may temporarily occluded, to the branchial arch or to its base. It appears that for some time after the atta ment, before the head of the parasite has been buried in the tissue of the gill arch, it is able to leave host. The fishes examined during the tank experiments had an average number of 22 parasites (14- on the gills, if they were fished out from the tank alive. Some fishes died during the night and w examined the following morning, several hours after death. These were found to have an average num of 8 (2-13) parasites on the gills. This suggests that at least some parasites were able to leave the dy host.

Once the head of the parasite has been buried in the tissues, further development takes place consists mainly in a differential and extremely pronounced growth of the genital segment, which elong considerably and becomes flexed into the typical form, accompanied by swelling. The part of the b which is described usually as the 'neck' pushes the head into the tissues of the host, until it reaches proximity of a large blood vessel; the head anchors in the walls of this, whence the parasite derive food, the blood of the host, by active sucking. The head is kept in position by the development of th cephalothoracic antlers, one dorsal and two lateral, which are usually more or less branched and wh make it impossible to pull out the head of the parasite without damaging it. The attainment of definitive form of the body is followed rapidly by the development of the egg-strings. The period of production, which now begins, continues throughout the remainder of the parasite's life.

LIFE SPAN

The life span of *Lernaeocera* is as yet not accurately known. Sproston and Hartley (1941) consi that the parasite spends no more than about eight weeks on its final host, Stekhoven (1936; Stekho and Punt, 1937) believes it to live on it for about one year, while Capart (1948) estimates its life spa extending to over twelve years. The main difficulty in assessing the life span is the impossibility of di observation and the necessity to apply indirect inferences.

A fresh assessment of the life span has been made by studying the composition of the parasite popu tions, both on the intermediate and on the final host. A large number of larvae (over 11,000) an second stage adult females (over 8,000) have been examined.

The larvae and the young mature females and males were collected from 221 lemon soles caug over twenty various localities, both inshore and offshore, in 1955 and 1956. The adult females (sec stage) from the haddock were examined in the catches landed in Aberdeen Fish Market (about 40 fish). The parasites have been classified into substages, according to the modified method of Spros and Hartley (1941) as follows:

P—'Penella' substage (parasite straight and colourless);
U—The flexure developed, but the parasite still thin and colourless;
W—Fully mature form attained, but no egg-strings present;
X—Egg-strings present;
Z—Parasite dead. Only fragments of the neck protruding from the host tissue.

From observations on the relative abundance of the various stages of development on the intermediate host and various substages on the haddock some estimation of the duration of these stages can be attempted (Fig. 2). The duration of the substage P, for example, can be taken roughly as the distance

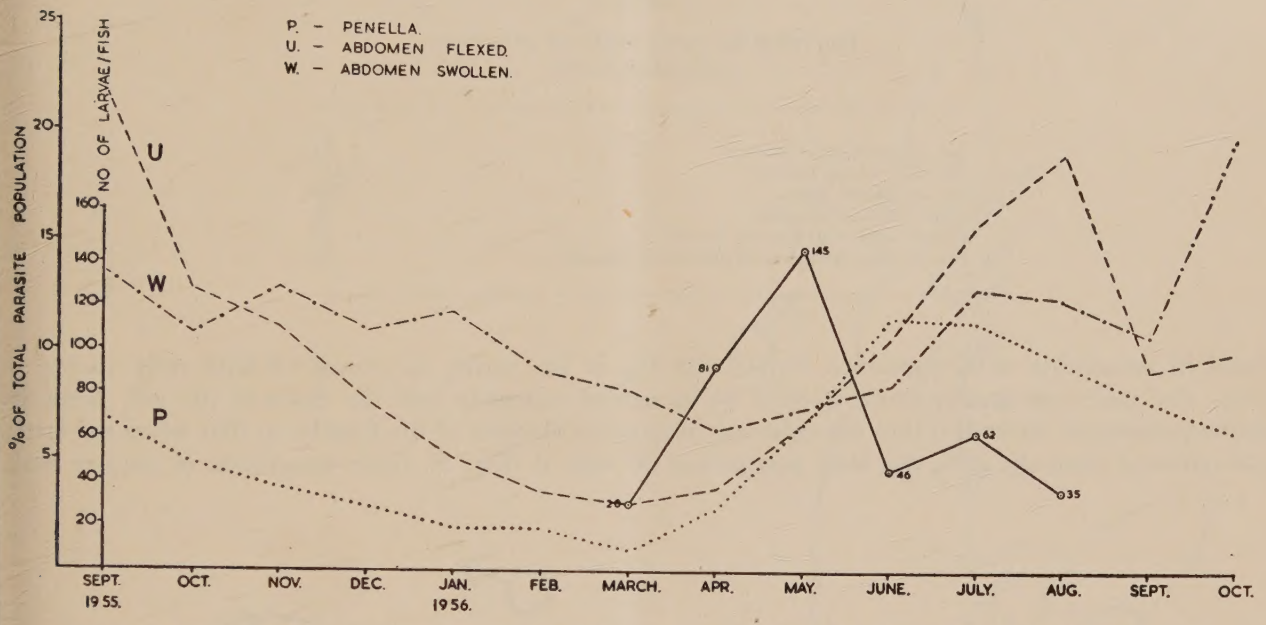

Fig. 2 Relative abundance of various substages of adult *L. obtusa* on the haddock and that of larvae on the lemon sole.

between the peak in the abundance of this substage and that of the next substage U. By this method the following durations can be established for various stages in the life cycle of the parasite:

Period spent on the intermediate host, about 6 weeks (4-8 weeks);
Duration of stage P – – about 6 weeks (4-8 weeks);
Duration of stage U – – about 8 weeks.

The duration of substage W cannot be determined by this method but, if the relative abundance of this substage is considered, it appears that its duration might be regarded as being about the same length as that of stage U. This suggests that the period between hatching and the beginning of the production of eggs is about six to seven months. Seven months is rather a long period for attaining the reproductive age in a copepod, but in view of the facts discussed later (p. 14) it can be accepted as approximately correct. The period between the deposition and the hatching of the eggs has been established for *L. branchialis* by Capart (1948) as being 8-15 days. This period perhaps can be assumed also for *L. obtusa*.

In the section on distribution data are presented which lead to the conclusion that the life of *L. obtusa* on the haddock extends over a period of about $1\frac{1}{2}$ years, so that the reproductive period of the parasite can be assumed to last for about a year.

REPRODUCTION

The female of *L. obtusa* is impregnated by the male while on the gills of the intermediate host. Some authorities maintain (Lajman, 1949) that fertilisation takes place in the free-swimming phase, which follows detachment from the flatfish, but this cannot be seriously considered.

Some light can be thrown on the mating behaviour by the examination of the data in Table I. In a large population of developmental stages of *L. obtusa* on 77 infested lemon soles, 159 mature males

and 68 mature females were found. Twenty-six males and females were found *in coitu* (which sho incidentally that copulation does occur on the gills of the intermediate host). The typical attitude copulation is shown in Fig. 4. An interesting feature, however, was the relatively large number of ma

TABLE I

Illustrating the mating behaviour of *L. obtusa*.
Explanation in text.

No. of lemon soles infested	77
No. of *L. obtusa* present	3,127
No. of mature males	159
No. of mature females	68
No. of males and females *in coitu*	26
No. of males attached to immature females	56

found in association with immature females (35·2% of the males, as compared with only 16·5% *coitu*). The male was usually firmly hooked by its second antennae into the tissue of the gill, while chelae penetrated through it into the chitinous anchoring filament of the female, so that when the lat was removed from the gills, the male was pulled off with it (Fig. 3). Such association of mature ma

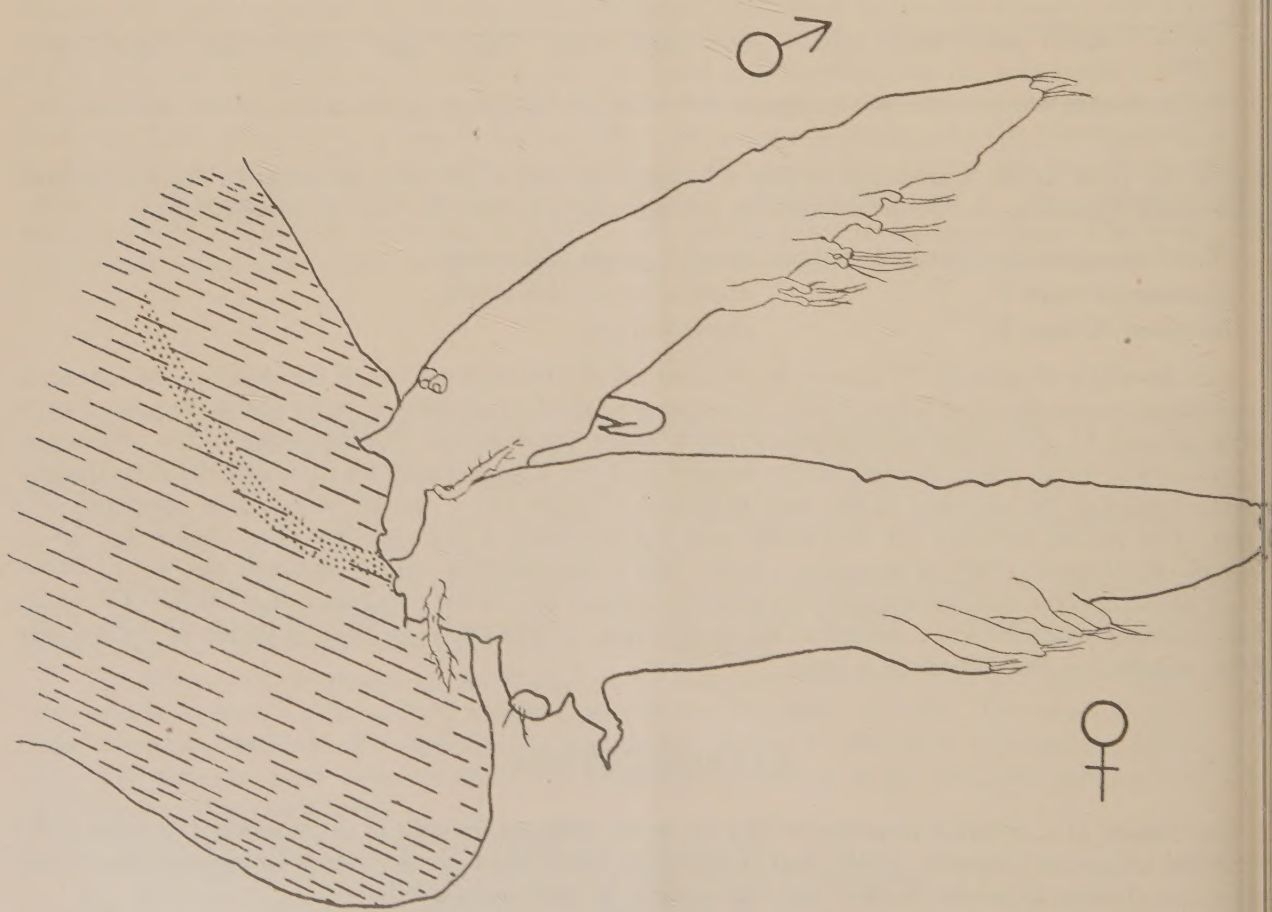

Fig. 3 *L. obtusa* in "pre-copulation" attitude (microprojector drawing).

Fig. 4 *L. obtusa* in the characteristic attitude of copulation (microprojector drawing).

with immature female seems to be not unusual among free-living copepods (Fraser, 1936; Gurn 1932; Perkins, 1956), but has not so far been observed among the parasitic species.

Males in this typical attitude have been found mainly associated with the older chalimus sta (chalimus III and IV), but on some occasions also with the earliest chalimus or even copepodite. T male in its search for a female must tend to associate with the first one it encounters, which may expl why relatively so many males were found with immature females while some of the mature fem (38·2%) were found without male company. The male, once attached to the immature female, proba remains in the 'preparatory' position (Fig. 3) until the female matures and can be fertilised. This wo suggest that the duration of the mature male stage must be much longer than that of the mature (stag female on the intermediate host. This is corroborated by the fact that the mature males are more t twice as abundant on the gills of the flatfish as the mature females. (The opposite generally obtain the adult populations of parasitic copepods.) Males have also been found attached to females in typical attitude of copulation, and even in the 'pre-copulation 'posture, on the gills of the hadd The first could be explained by failure of the male to detach itself from the female after copulation, it is also possible that a male, which left the gill chamber of the flatfish without copulating, attempt do so on the gills of the final host. This certainly seems to be true in the second case.

The main feature of the reproduction of *L. obtusa* is that it is not confined to one or more sha defined reproductive seasons; it carries on—with flunctuations in intensity—throughout the year. intensity of egg laying at any given time of the year can be determined by the numbers of larvae fo on the gills of lemon sole and—though less directly—by the number of 'penella' substages on the of the final host. The latter is a less reliable indicator on account of the mortality occurring betw departure from the intermediate host and arrival on the final host. This mortality might be sub to fluctuations and is very difficult to determine.

In contrast to many other copepods, neither *L. obtusa* nor *L. branchialis* empty their egg-str speedily. The deposition of eggs is a continuous process, and the eggs extruded by the female into end of the strings are discharged at the other; otherwise one would expect to find individuals with en strings. Sproston and Hartley (1941) found only two such individuals among all the parasites they ex ined and deduced that death must follow quickly on the cessation of reproductive activity. In se thousands of parasites examined by the present author no such individuals were encountered. S dead parasites, already beginning to disintegrate, still carried fragments of half-filled egg-strings.

The eggs of *Lernaeocera* hatch, according to Capart (1948), in 8-15 days. They are not pelagic probably do not meet with great environmental differences throughout the year, as the physical

TABLE II

Intensity of infestation of lemon soles with larval *L. obtusa* in different months.

Stage of development	March		April		May		June		July		August	
				(A) Absolute numbers/fish								
Copepodid		18·3		44·9		53·6		29·8		42·9		9·9
Chalimus I	4·5		14·8		30·4		8·2		11·7		16·8	
Chalimus II	1·0		5·6		13·0		2·2		3·3		2·8	
Chalimus III	0·7	7·8	4·3	31·0	9·6	70·1	1·7	13·6	2·2	18·8	2·0	23·3
Chalimus IV	1·6		6·3		17·1		1·5	—	1·6		1·7	
Adult ♂	1·6		4·1		12·9		1·6		2·3		1·8	
Adult ♀	0·7	2·3	0·9	5·0	8·0	20·9	0·9	2·5	0·6	2·9	0·1	1·9
				(B) % of different stages/fish								
Copepodid		64·4		55·5		37·1		65·0		66·3		28·2
Chalimus I	15·8		18·3		21·0		18·0		18·1		47·8	
Chalimus II	3·4		6·9		9·0		4·8		5·1		8·1	
Chalimus III	2·4	27·1	5·4	38·3	6·6	48·5	3·6	29·6	3·4	29·0	5·7	66·4
Chalimus IV	5·6		7·8		11·8		3·2		2·5		4·8	
Adult ♂	5·7		5·1		8·9		3·4		3·6		5·0	
Adult ♀	2·6	8·4	1·1	6·2	5·5	14·4	1·9	5·4	1·0	4·6	0·4	5·4

tions at the bottom of the sea are fairly stable. Probably there are also no great variations in the length the incubation period.

Fig. 2 shows that the period of maximum intensity of reproduction, as determined by the number of rvae on the lemon sole, reaches its peak in April-May. This agrees with Stekhoven's observation on e infestation of flatfishes by *Lernaeocera* in the Belgian coastal area. The maximum intensity of egg position apparently precedes the maximum period of infestation of the flatfish by about a fortnight.

In the course of the present work the infestation of lemon sole was studied from March to August 56. It was felt that this time should cover the maximum infestation period. The results are summarised Table II and show the occurrence of two major changes in composition of the larval population. March the population was relatively young, copepodids constituting more than half of it and mature rms less than one tenth. The population became progressively more mature and abundant between arch and May, when the peak was reached. In May the copepodids became reduced to only one-ird of the population, while the combined percentage of pupal and mature forms was about double at of March.

The first sudden change occurred between May and June, when the mass transfer to the final host ok place. The absolute intensity of infestation dropped very considerably and the population became atively younger again, the percentage of copepodids rising to the March level. At the same time the mber of 'penella' substage on the haddock rose to its peak.

Recruitment increased in July, after which the second major change occurred, resulting in the eing of the populations of parasites, which was accompanied by a further decrease in abundance. is time the ageing of the population was due to the large drop in the rate of recruitment, the adult aximum occurring perhaps in September.

The reproduction during the remainder of the year was determined by observing the abundance of e 'penella' substage on the haddock (Fig. 2). The steady decline of the rate of reproduction can be de-ced from the gradual drop in the 'P' line, indicating the decrease in the rate of infestation of haddock m the months June-July. This decrease continued till March, when the mass deposition of eggs begins d the cycle of events is once again repeated.

All these observations were completed within one year. It is quite feasible that the reproductive ivity might differ from year to year, but the deviations from the picture presented above are probably all.

DISTRIBUTION

ographic Distribution

The geographic distribution of any animal depends on its environmental requirements. The wider range of tolerance the wider territory it is likely to inhabit. The environment of a parasitic animal n be subdivided into

(i) the immediate environment provided by the host, in whole or in part;

(ii) the outer environment in which the host lives.

e geographic distribution of *L. obtusa* should be regarded as dependent on the following factors:

1. Distribution and abundance of the intermediate host;
2. Distribution of the final host;
3. Physical conditions of the outer environment.

When it became clear that the distribution and the percentage incidence of *L. obtusa* on the haddock e no relation to the distance from the shore, contrary to expectation if the flounder were the main rmediate host, a search was made for an intermediate host which would permit completion of the cycle of the parasite in the open sea. It was found that 95% of the lemon sole population was infected h the developmental stages of *L. obtusa* (Kabata, 1957).

Some relationship between the distribution of *L. obtusa* on haddock and the centres of concentration he lemon sole was reported by the present author and has been investigated further. The first infor-tion was obtained from trawl skippers fishing from Aberdeen, who observed that more parasitised

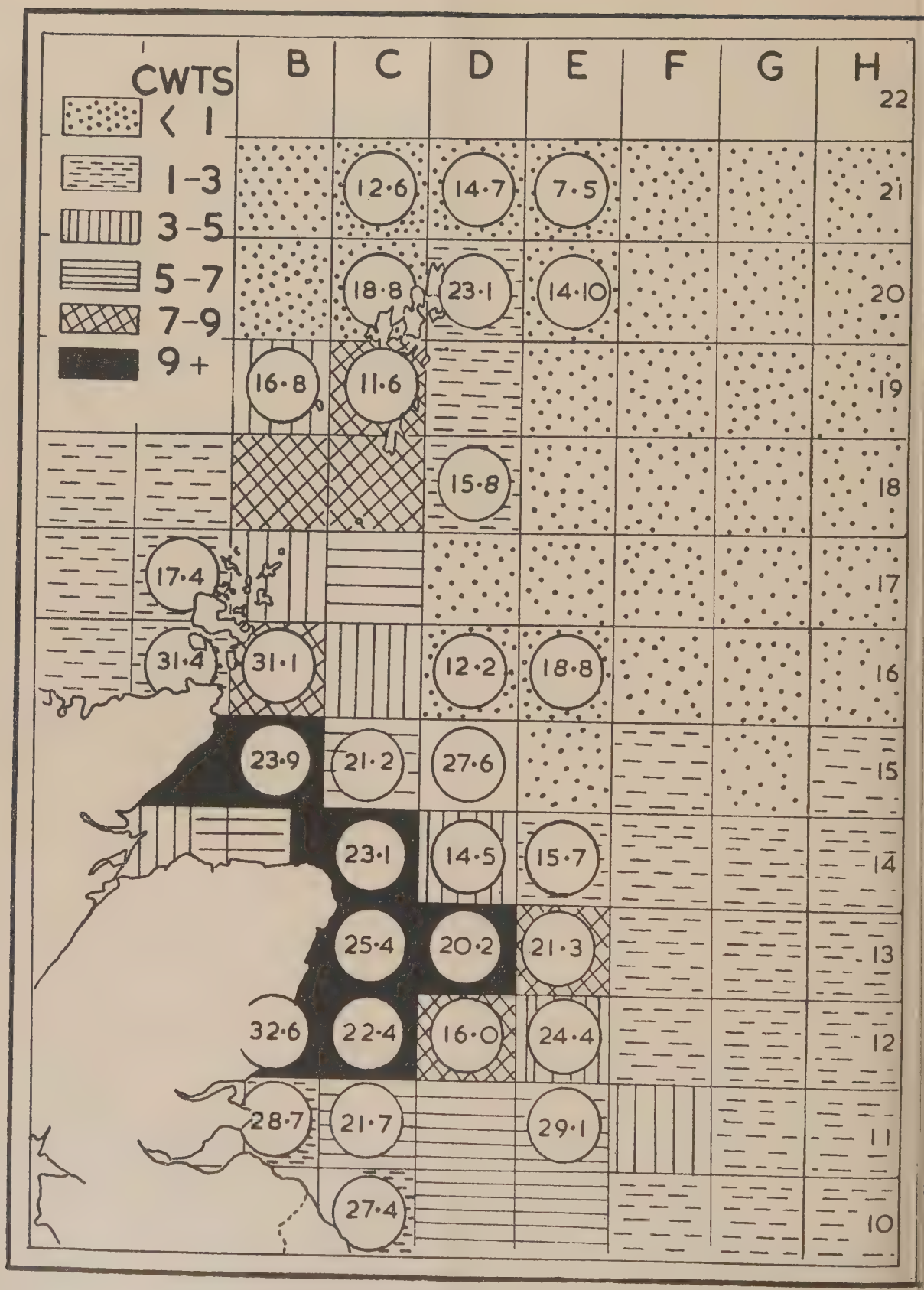

Fig. 5 Distribution of the lemon sole (expressed as cwt/100 hrs fishing) and its relationship to the incidence of *L. obtusa* on the haddock, shown as percentage infestation in each square.

haddock were caught on the grounds where lemon sole was abundant. As a basis for a more quantitative check, the distribution of the lemon sole, as worked out by Rae (1939) was used. The data in Fig. 5 are the catches of lemon sole in cwts/100 hrs fishing by commercial trawlers from Aberdeen in the years 1923-1936, superimposed on which are the records of incidence of *L. obtusa* on haddock examined during 1956. The distribution and abundance of lemon sole does not undergo substantial fluctuations and has not significantly altered between the period on which the map was based and the present day. Fig. 5 shows that the percentage of infestation of the haddock tends to rise with the increase of the abundance of the lemon sole on the grounds. In fact, one can regard it as being about doubled with a tenfold increase in the abundance of the lemon sole. These results of course, must be treated with caution. Both haddock and lemon sole, although not excessively migratory species, are by no means so sedentary as to remain confined within one statistical square. A haddock infested in one square might be captured in another. Even the roughest correlation is therefore valuable.

The geographic distribution of the final host is the chief factor determining the geographic distribution of the parasite. In the case of *L. obtusa* the distribution of the parasite extends throughout the northern and possibly also much of the southern North Sea, but the stocks of haddock outside the European continental shelf, e.g. in Faroese and Icelandic waters, are free from *L. obtusa* (Kabata, 1957). The fact that this parasite has never spread to those waters might be explained by the inability of its hosts, both haddock and lemon sole, to negotiate the deep water barriers. It must also be mentioned that the abundance of the parasite within the northern North Sea does not seem to be related to the abundance of haddock on the ground. This has been checked in the same fashion as the correlation between the lemon sole and the incidence of the parasite. A chart of the quantity of haddock caught per 100 hours fishing has been compared by the author with the chart of incidence of *L. obtusa* and revealed no relationship between the density of haddock population and the abundance of the parasite.

The third of the factors determining the distribution of *L. obtusa*, the physical conditions of the environment, has not been investigated, but it must be borne in mind that this factor might be instrumental in excluding this species from the areas north of the European continental shelf.

DISTRIBUTION ON THE HOST POPULATION

Because the parasite reproduces and spends its entire life cycle in the open sea, its final host—the haddock—is, unlike the whiting and the cod, exposed to infestation throughout its entire life, unless it lives outside the area occupied by the intermediate host. It has been mentioned in an earlier section that the peak of infestation of the final host falls in the months June-July. Haddock in the first year of life are pelagic till about August and by the time they become demersal the peak of infestation has passed and the young fish are less vulnerable to infestation till the next peak. Coupled with this is the fact that the small fish offer a smaller surface to the parasite, which might also favour their relative immunity during the first year of their life.

During the period 1946-1949 some data on distribution and abundance of *Lernaeocera* were collected by Mr. B. B. Parrish of this laboratory. His data have kindly been placed at the author's disposal and show that of 1,782 haddock of 0+ group examined by him in 1947-1948 not one individual was infested.

During the second year of life haddock reach marketable size and from this age onwards can be easily examined from the commercial landings. In Aberdeen Fish Market haddock are segregated into four size categories: small, medium, large and extra large. The average age of haddock in each of these categories is as follows:

	Age (years)	
	Range	Mean
Small – –	1 - 5	2+
Medium – –	2 - 6	3+
Large – –	2 - 8	4+
Extra Large –	No data	5 and over

These data are based on an analysis of the age composition of commercially caught haddock in 1956.

About 40,000 haddock were examined in the Aberdeen Fish Market for the incidence of *Lernaeocer* between the second half of 1955 and the end of 1956. The average infestation of the entire populati during that period was 18·7%. The infestation was not, however, the same for all the size categori The figures below show the differences in the extent of their infestation.

	Examined	Infested	% Infested
Small – –	20,470	3,079	15·0
Medium – –	12,061	2,614	21·7
Large – –	5,701	1,474	25·8
Extra Large –	648	185	28·5

It is evident from these figures that the infestation incidence is related to the size and age of the fis Haddock of five years and over appear to be infested twice as much as those of two years old. The proble arises: what is the reason for this trend in incidence of infestation?

At this point it is useful to discuss data mentioned earlier (p. 7) in the section on the life span. has been stated there that the estimated duration of life of *Lernaeocera* on haddock is about $1\frac{1}{2}$ year If we assumed a life span of several years duration for this parasite, then we should have to expect th the older fish, having been exposed to infestation longer than the young ones, would accumulate parasit throughout their life and thus come to be more heavily infested. The percentage infestation quot above would then appear to indicate a tendency for the rate of infestation to decrease with the grow of the fish. However, unless the fish moves outside the area inhabited by the intermediate host as it ag there is no reason why the older fish should be infested at increasingly lower rate. All the fish examin were caught well within this area. The habitat of the fish does not alter significantly, neither does— far as we know—its physiochemical regime. The surface exposed to infestation increases in size. T only deterioration of the position from the parasite's point of view is the increase in the distance whi must be travelled to obtain access to a suitable blood vessel.

If the fish continues to be infested by long-lived parasites, then we might expect the parasite popul tion of older fish not only to be larger but also to contain relatively more old individuals than the popul tion of a younger host; especially so if no changes occurred in the rate of infestation. A population parasites was analysed to investigate this possibility. The following numbers of parasites were examine

From small haddock	–	–	3,650
From medium haddock	–	–	3,329
From large haddock	–	–	2,070
From extra large haddock	–	–	299

The results of this analysis are shown in Table III. The first thing attracting immediate attention that no accumulation of fully developed (substage X) parasites has taken place, the percentages of tho parasites being the same for the small and the extra large category. Generally speaking, the age comp sition of the parasite populations from the different size categories is roughly the same, although ext

TABLE III

Percentage composition of the parasite populations on haddock of different sizes.

Stage of parasite	Size category of haddock			
	Small	Medium	Large	Extra large
P	5·42	1·44	5·41	2·34
U	8·32	9·13	8·69	7·36
W	9·62	10·27	9·66	7·69
X	64·41	63·23	59·95	65·89
Z	12·22	15·92	16·28	16·72

ge haddock are about twice as heavily infested as the small. This implies a large overturn within population, with the parasites dying and being replaced at a relatively high rate. That this is so n be seen from the percentage of dead (substage Z) parasites in the populations of the different sizes fishes. This percentage is 12·2 in the small haddock and 16·7 in the extra large, a relatively small rease. It is especially interesting that even the small haddock, of average age 2+, carry the dead re- ins in numbers which are far too high to be accounted for by accidental deaths. The consideration the data shown in Table III leads to the conclusion that the life span of *L. obtusa* on the haddock is ween 1 and 1½ years, probably nearer to the latter period. The fish, then, must be liable to reinfestation the parasites at an increasing rate, if the pattern of incidence is to be maintained. The larger fishes st be infested at about twice the rate of the small ones. Such differences in the rate of infestation are unusual in the host-parasite relationship. The pattern of infestation differs strikingly from that cribed by Poulsen (1939) for *Clavella* and indicates complete absence of immunity against the parasite.

Table IV gives data about the rate of infestation of size categories. If the average number of parasites the total population is considered, it may be seen to increase 2½ times from small to extra large fish, ile at the same time the increase in the average number of parasites per infested fish is from 1·2 to , i.e. about a quarter.

TABLE IV

Infestation of haddock of different size groups.

	Small	Medium	Large	Extra large
No. of fish examined	20,470	12,061	5,701	648
No. of fish infested	3,079	2,614	1,474	185
Total number of parasites	3,872	3,725	2,252	320
Average no. parasites/fish examined	0·2	0·3	0·4	0·5
Average no. parasites/fish infested	1·2	1·4	1·5	1·7

TRIBUTION IN TIME

Infestation of haddock with *L. obtusa* appears to fluctuate from year to year. The author's own ervations have not continued long enough to form a clear picture of such fluctuations, but in con- ction with the data obtained by Mr. Parrish in earlier years they are sufficient to show that such tuations exist. The following overall incidence of infestation of haddock has been determined:

For 1946 – – 24·1%
For 1947 – – 8·1%
For 1948 – – 4·9%
For 1955/56 – 18·7%

The relatively high percentage of infestation in 1946 can be explained by the fact that the data ected in that year were mainly from the areas with a generally high incidence of infestation and a d stock of lemon sole. To compare the abundance in the above years three areas have been chosen, three of generally high infestation incidence. The results of this comparison are shown in Table V.

TABLE V

Fluctuations in percentage of infestation of haddock with *L. obtusa* in different areas.

Area	1946	1947	1948	1955/56
C 13	22·6	4·7	2·4	25·4
C 11	36·0	15·9	9·9	21·7
B 11	30·3	24·0	16·8	28·7

It will be seen that relatively the same differences obtain for individual areas as for the total data. infestation seems to have been highest in 1946, then suddenly decreased in 1947. The decrease conti in the following year. From 1948 till 1955 no data were available but in the latter year the percen was much higher. No reasons for these fluctuations are known.

MODE OF ATTACHMENT

L. branchialis is stated by earlier workers (Stekhoven, 1936) to be attached to the anterior wall o gill chamber. Stekhoven doubts even whether this species should be regarded as a gill parasite at a

L. obtusa attaches itself in the gill chamber of the haddock, either to the wall of the chamber o the surface of the branchial arches and from these points penetrates to the proximity of a major b vessel, in the wall of which its head becomes embedded.

The mode of attachment of *L. obtusa* has been studied by the present author in a sample of females from the haddock. The results are presented diagrammatically in Fig. 6. Each vertical ba the diagram represents a gill bar divided into four parts which, with the base of the arch and the immediately above the arch makes six sectors, horizontally dividing the gills. The largest numbe

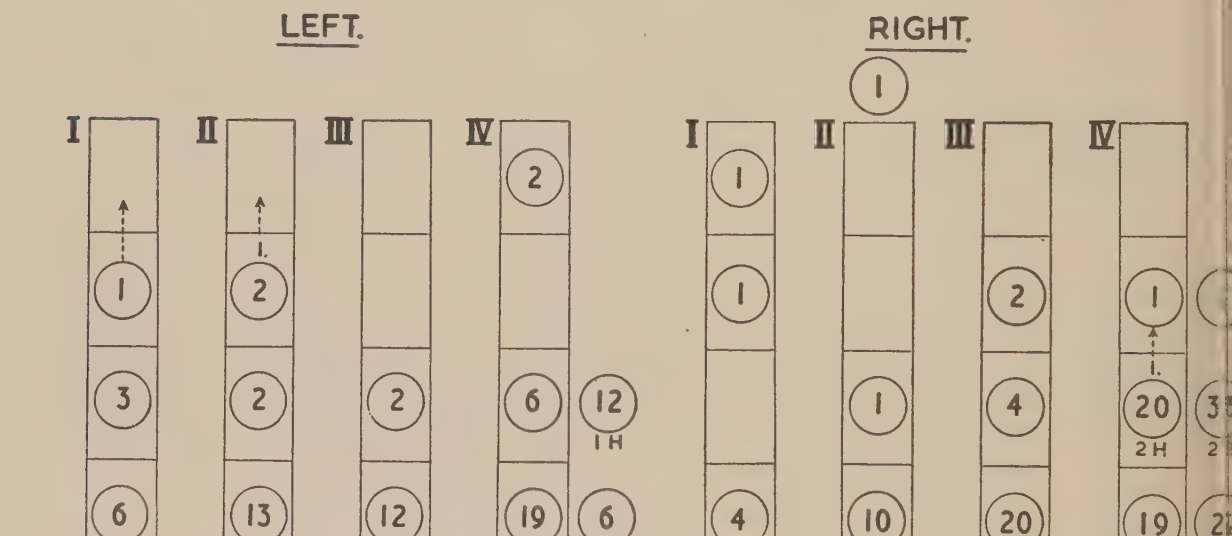

Fig. 6 Distribution of *L. obtusa* on the gills of haddock. Explanation in text.

parasites was found to be attached to the second lowest sector (the gill area directly above the bas the arches), where 103 out of 295 parasites were found. Slightly less than half of all the parasites exami here were attached to the gill arches, the remainder being attached to the area at the base of the arc and posteriorly behind the arches. The majority of parasites attached to the arches cannot, howe be said to be parasitic on the gills, since the heads of these parasites are embedded in the wall of ventral aorta, the gills constituting only the point of entry into the tissues of the host. The aquari experiments show that the parasite alights on the surface of the gills, usually on the tips of the gill f

nts, slowly making its way along the filament towards the arch. Fig. 6 shows that most of the parasites ch penetrated the bulbus arteriosus of the host (marked H), were attached either to the last gill arch directly behind it. Vertically, some of those parasites were situated near the middle of the gill bar ut of 19) while 12 were found just above, and two below, the base of the arches. Some of the parasites rked P) penetrated from one branchial chamber to the opposite one. Some again, especially those ched higher up the arch, had necks which grew along the arch and heads which became finally edded in a different sector of the arch from the one at which the attachment took place. These are icated in the diagram by the arrows. Only one parasite was embedded above the gill arches.

When the numbers of the parasites attached to various gill arches are considered, it becomes clear t the largest concentration is to be found in the postero-ventral quarter of the gill chamber. This is place which would be preferentially infested by a parasite entering the chamber from outside against opercular current and not with the water passing over the gills. This lends support to the supposition the parasite seeks out its host with the help of positive rheotropism. That the parasite is able to enter gill chamber in this way can be appreciated on observing live mature *Lernaeocera* swimming in the arium tank. The parasite moves in typically copepod fashion, by means of short and rapid jerks. s mode of progress is, however, occasionally interrupted by a sudden burst of great speed which ies the animal over a fairly long distance (a foot or so) in one smooth motion. This motion seems to nore than sufficient to counteract the opercular current and effect the entry into the gill chamber.

PART TWO

Effects on the Host

INTERMEDIATE HOST

The demands made by every living organism on its environment vary with the degree of develop- t of that organism. The differences may not only be quantitative but also qualitative. A parasite may ge its feeding habits from one developmental phase to another and may be at various stages of the cycle more or less dependent on the host. As a rule, demands placed on the host are greatest during hases of vigorous metabolic activity (e.g. reproductive period) of the parasite which at such times s to be more rigidly specific.

Larval stages of *L. obtusa* inhabit the gills of the lemon sole, and the main ways in which the activities e larvae become injurious to the gills are by attachment and feeding. The first results in the irritation, acement and some destruction of the tissues of the gills by the insertion of the anchoring filament; econd, if the structure of the mouth parts of the larvae is any indication, causes superficial abrasions.

The reaction of the gill tissues to any harmful stimulus is remarkably uniform. Irrespective of the re of the stimulus (i.e. whether it is mechanical, chemical or thermal) the tissues react by hypertrophy äperclaus, 1954). The process begins in the grooves between the respiratory folds and results in the plete obliteration of these folds from the affected area, thus influencing to some extent the facility e gaseous exchanges of the host. Fig. 7 shows tips of five filaments, four (A, B, C, D) showing the ts of infestation and one (E) uninfested. The changes shown by the infested filaments cannot be uted to a single parasite and must be regarded as the result of repeated and multiple infestations. largest number of larvae found on one fish was 577, with up to 10 larvae on a single gill filament. response of the gill tissue is shown very clearly by the four filaments illustrated. The respiratory

folds disappear and the tip of the filament swells, on some occasions sprouting new tips and in extr cases assuming a 'cauliflower' formation. The tips split and a considerable area of respiratory fol destroyed, in severe cases amounting to almost half of the filament.

In spite of the damage to the tips of the gill filaments, the total loss of respiratory surface is prob not large enough to result in any serious changes in the respiration of the fish. Since the abrasions o gill surface caused by the feeding are only injuries of local and limited extent, it may not be unreason to assume that *L. obtusa* exerts no great effect on the lemon sole.

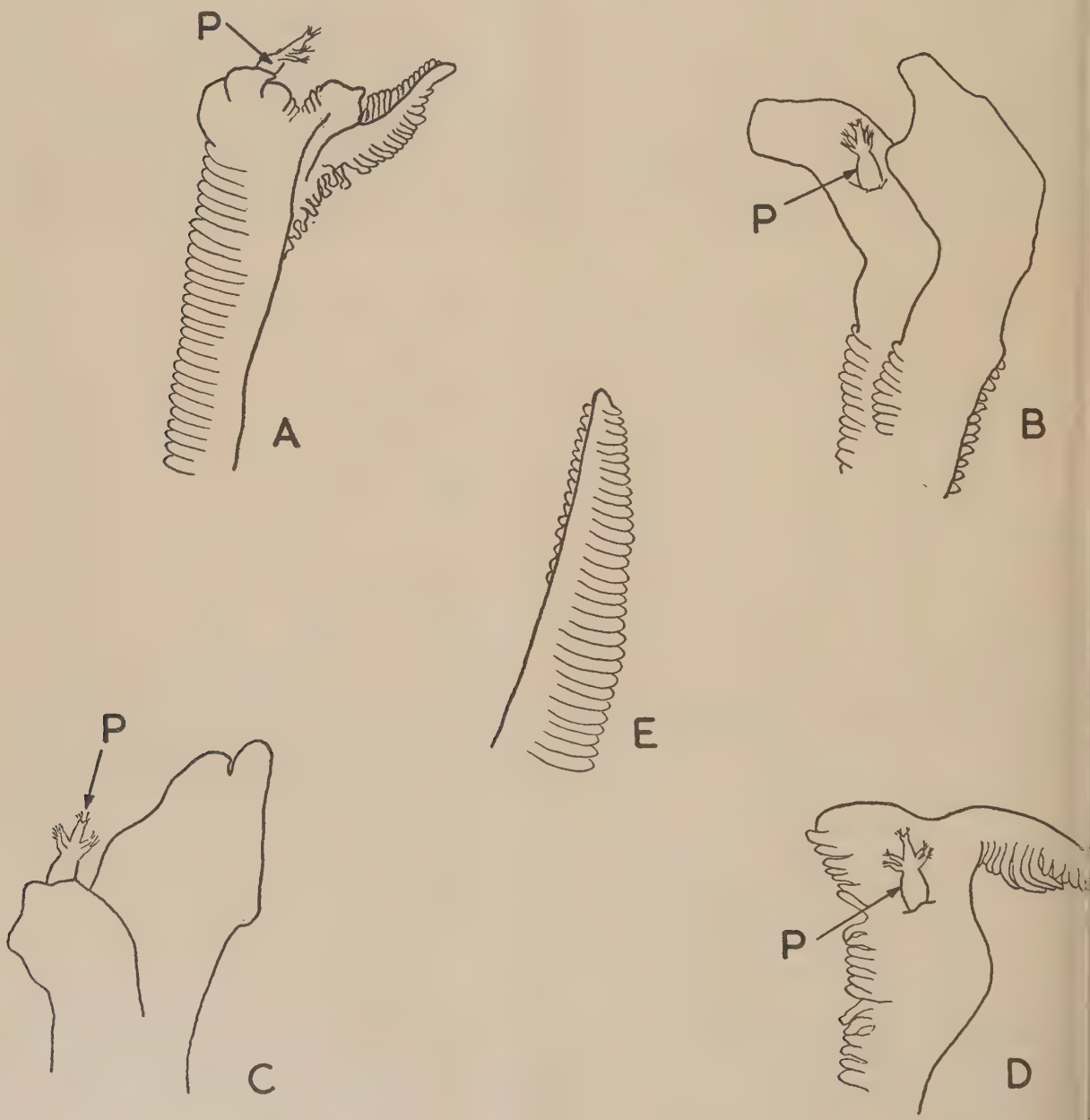

Fig. 7 Showing the effect of infestation with larval *L. obtusa* of the gills of lemon sole. A, B, C, D—infested gill filaments (parasite indicated by P); E—uninfested filament.

FINAL HOST

As with the intermediate host, the final host is affected by the following phases of parasite's activity:
(a) attachment, resulting in destruction and dislocation of tissue;
(b) feeding, resulting in the loss of tissue (blood).

The penetration of the head and neck of the parasite into the tissues of the host provoke reactions which have been described for *L. branchialis* by Stekhoven (1936). The wall of the blood vessel undergoes hypertrophy with considerable increase of vascularisation of the affected locality. The newly formed capillaries ensure sufficient blood supply for the parasite, which does not penetrate into the lumen of the vessel but derives its food from the wall of the latter. Some local necrosis of the tissues occurs, but the area of penetration becomes isolated from the remaining tissues by the formation of a capsule, which surrounds the head and the neck of the parasite.

The effects on the host of the displacement of the tissues, and their destruction caused by the attachment of the parasite, might be regarded as local and without serious effect on the general well-being of the host, unless the hypertrophy should occur in or near the heart and occlude or seriously reduce the lumen of an important blood vessel. In such cases some general disturbances of circulation might take place, but these are perhaps rather exceptional. The main effects on the host can be attributed to the feeding activity of the parasite. The loss of blood due to one parasite, which has been estimated as being about 100 mm^3 every eight days (Sproston, 1941; Capart, 1948), is bound to have serious results, especially in smaller fishes. The effects of such a continuous drain on the resources of the fish must be widespread and noticeable in many aspects of health. To assess their extent and degree the following details were investigated:

(a) Changes in the haemoglobin content (anaemia);
(b) Liver fat content;
(c) Weight of the fish;
(d) Growth of the fish;
(e) Sexual development of the fish.

CHANGES IN THE HAEMOGLOBIN CONTENT (ANAEMIA)

The first and the most obvious result of continuous loss of blood is the appearance of secondary anaemia with all its implications. Very often an infected haddock can be recognised at the first glance by the changes in the coloration, which can be described as 'pallor'. The usual dark, purplish red colour of the skin of the head in the area between and around the eyes is replaced by pale grey.

Anaemia induced by the infestation with *Lernaeocera* was first studied by Mann (1952), who observed the erythrocyte count and the haemoglobin content of the normal and infested whiting. His results are shown below:

	Haemoglobin content	Erythrocyte count
Normal whiting – –	38-40%	902,500
Infested whiting – –	20-22%	847,500

These figures are based on ten observations each for the haemoglobin content and the erythrocyte count. Mann did not state what standard he accepted for 100% haemoglobin; it might be assumed that the usual 14·8 g/100 cc of blood was used.

During the present work an attempt was made to determine the extent of anaemia caused by *L. obtusa* in the haddock. Because of the necessity to take observations on the fresh blood at sea, it was not possible to undertake the erythrocyte count. For the determination of the haemoglobin content Sahli's haemoglobinometer was used. In all, 69 observations were taken, 27 in March 1956 and 42 in March 1957. To determine the influence of parasitisation some observations were taken from each of the following categories of fish: uninfested, infested with immature parasites (substages P and U), with one mature (substage X) and with two or more mature parasites.

The average percentage haemoglobin content for these categories, obtained in March 1956, wa

Average uninfested – – – –	38·3%
Average infested with immature parasites – –	46·7%
Average infested with one mature parasite – –	31·9%
Average infested with two or more mature parasites –	27·5%

The most interesting feature of these observations is the rise of haemoglobin content in the fishes infest with immature parasites. It appears that the loss of blood stimulates the body of the fish to compensato reaction which at the intitial stages overshoots the normal level of the haemoglobin content. Th phenomenon is not unusual in man.

It is interesting to record that histological examination of several spleens from infested and uninfest haddock did not reveal any noticeable changes in the tissues of this the main haemopoietic organ.

Further observations on the haemoglobin content were made in March 1957. To minimise an possibility of seasonal fluctuations in the blood picture, the same month of the year was chosen. Th following values were obtained:

Average uninfested – – – –	38·4%
Average infested with immature parasites – –	47·0%
Average infested with one mature parasite – –	24·1%
Average infested with two or more mature parasites –	19·2%

The most interesting features of these observations are:

(i) the very close agreement between the percentage of haemoglobin content in uninfested fish and those infested with immature parasites in 1956 and 1957 and agreement between th values for the uninfested haddock and Mann's normal whiting;

(ii) full confirmation of the rise in the haemoglobin content with the onset of infestation;

(iii) the lower values for the fishes infested with mature parasites in 1957.

The last might be due to experimental error, giving too high haemoglobin content to the fish examin in 1956, but it might also be due to the existence of a quite considerable range of values for the haem globin content in haddock of this category, dependent on the length of time during which the fish h carried a mature parasite.

The loss of haemoglobin is bound to affect the respiration of the fish. Mann experimented wi infested and uninfested whiting to establish the possible differences between the oxygen uptake of th two fishes. He determined that while the uptake of oxygen of uninfested whiting was 0·17 mg per g body weight, in the case of the infested whiting it was only 0·12 mg per g of body weight, i.e. a decrea of about 30%. It is very probable that this did not represent the extreme degree of anaemia, since th fishes in the extreme condition could not be used for the purpose of experiments, so that decreases over 50% might occur. Loss of blood and anaemia result in a slower metabolic rate and general sluggish ness, which in turn leads to decreased food intake and increased vulnerability to predators. To wh extent these factors might be responsible for an increase in the rate of mortality is difficult to assess a present.

Loss of blood, apart from causing anaemia, usually results also in decreased immunity again infections.

Liver fat content

General examination of the infested and uninfested fishes revealed that the former tended to ha smaller livers than the latter. Histological examinations did not show any gross structural changes i the livers of the infested fishes, but they did show the absence from these livers of the typical fat droplet Liver is the main fat depot of the haddock and any changes in the fat content of that organ can be take as reflecting the changes in the fat content of the whole fish. For this reason, the fat content of the liver of infested and uninfested fishes was examined.

The livers were removed from the fish and preserved in absolute methyl alcohol. An interval about three months elapsed between the preservation and analysis. The preserved liver was dried in

:uum oven and extracted by means of a Soxhlet extractor and 1 : 1 chloroform/methanol solvent. ıole livers were analysed, whenever their size allowed. Otherwise portions as large as possible were :d.

In all, 106 livers were analysed and the results can be summarised in the manner similar to that d for the haemoglobin content, expressing the total fat of the liver as the percentage of its weight:

Average uninfested – – – –	67·4%
Average infested with immature parasites – –	71·4%
Average infested with one mature parasite – –	57·8%
Average infested with two or more mature parasites –	32·6%

e first thing attracting attention is that these data tend to parallel the values obtained for the haemo- bin content (Fig. 8). With the onset of infestation the fat content of the liver tends to increase slightly, increase being followed by a drop, which in the case of the fishes carrying two or more mature parasites ves the fat content of the liver.

The increase in the haemoglobin content with the onset of the infestation is a normal phenomenon l can be attributed to the usual stimulation by haemorrhage of the haemopoietic organs and to the rshooting of the compensatory reaction. The mechanism responsible for the increase of the fat con- t is not readily understandable. The phenomenon itself is not generally known. The only record of ilar nature known to the author is the report by Petrushevski and Kogteva (1954) of the investigation Bazikalova in 1929 of the influence of direct infestation of the liver of cod by acanthocephalid worms. e figures obtained by Bazikalova, as quoted by Petrushevski and Kogteva, are as follows:

Numbers of worms in liver	% of fat
0 - 5 –	3·0
6 - 10 –	3·9
11 - 15 –	3·0
16 - 20 –	2·8
21 - 25 –	2·1

ese figures represent quite clearly an occurrence similar to that of the fat changes in the liver of *naeocera*-infested haddock.

ANGES IN WEIGHT

This aspect of the harmful influences of *Lernaeocera* on its gadoid host was first investigated by Mann 52), who examined cod, whiting and haddock and found that the infestation resulted in considerable of weight. The loss amounted to 20-30%. Mann's investigations showed that the loss ranged quite siderably (0-47%). This might be again due to the different degrees of development of the parasite different length of parasitisation. Some infested fishes show a higher condition factor than the average the uninfested ones. No increase of the harmful influences was observed with the increase in the age sh.

In the present investigation a sample of 248 haddock was examined to determine any changes in condition factor with infestation by *L. obtusa*. The condition factor was calculated in the usual way, the total weight of the fish was found by removing the stomach and gut content as carefully as possible ore weighing the fish, with all its internal organs. The percentage of underweight was determined by nn's method and the results are shown in Table VI. The sample was subdivided into the same cate- es as for the estimation of fat and haemoglobin content. Only the average condition factors are con- red but it must be mentioned that each category had a wide range of condition factor values and the ranges overlap. In fact, as in Mann's samples, the individual infested fishes quite frequently a higher condition factor than that of the average uninfested. The limitations of condition factor well known and we might assume that individual variability of shape, the differences of age, etc. some influence on the values. This work must concern itself with averages, and the average effects nfestation can be said to be definitely, but not drastically, harmful. The loss of weight is not as great

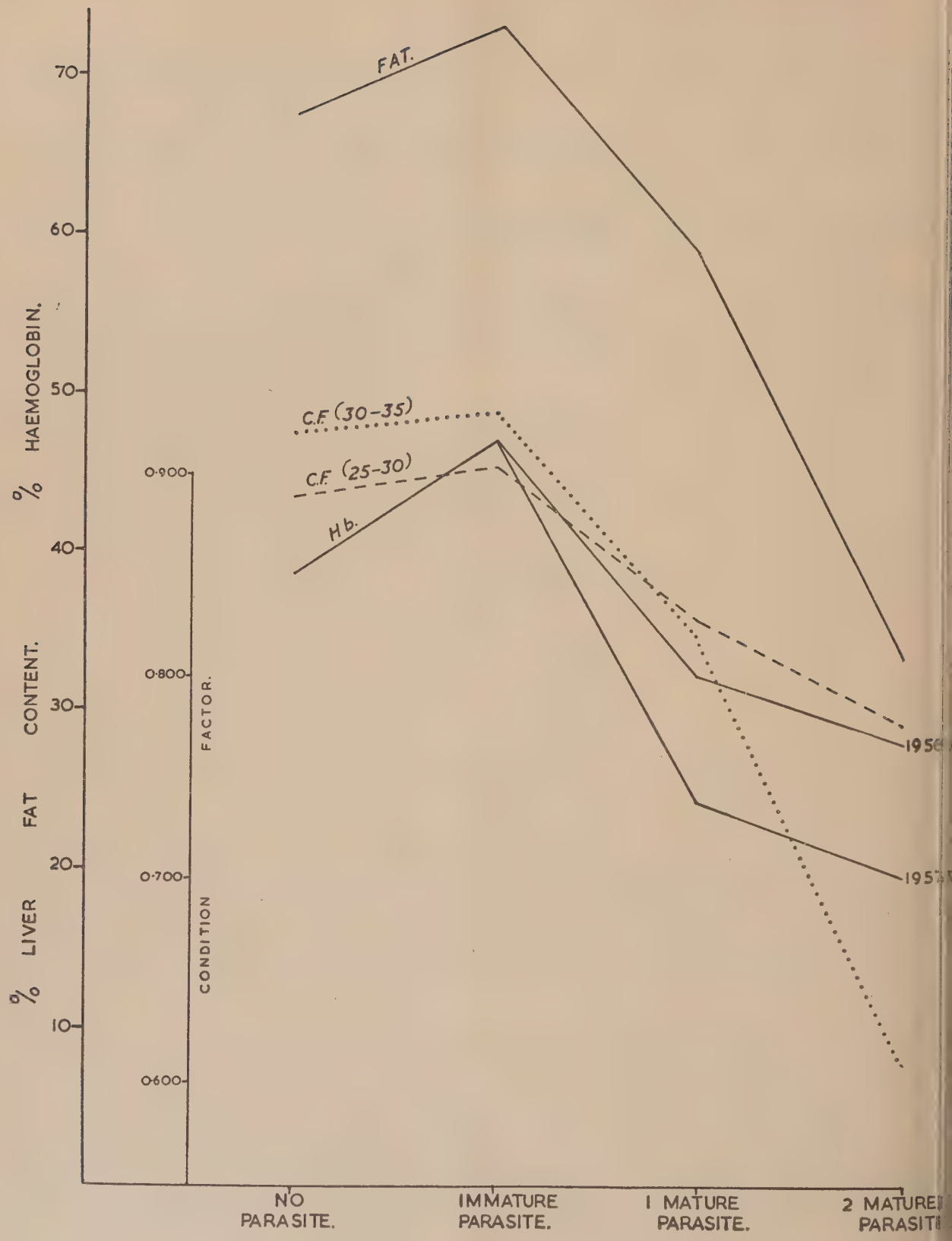

Fig. 8 Summarising the effects of infestation of haddock with *L. obtusa*. The values for haemoglobin content (Hb), fat content of the liver (FAT) and condition factor (C.F.) show initial increases followed by considerable drop.

that found by Mann. Only in the case of the fishes of the 30-35 cm length group (Fig. 8) is it near values calculated by that author; otherwise it was about 10%.

Fig. 8 shows that the average values for the condition factor of the fishes infested by the younger ges of the parasite are slightly higher than those for the uninfested. The increase is so slight that it ıld be entirely disregarded, were it not parallelled by the very similar increases in other values (haemo- bin content, liver fat). As it is, it can be said that with the onset of infestation the fish does not show immediate loss of weight and that perhaps some slight tendency towards the increase in weight might suspected.

The fishes bearing many parasites have not been examined in sufficient numbers to obtain repre- ıtative pictures. Two specimens were found bearing 11 parasites each. These specimens did not appear duly out of condition and certainly did not show the typical 'razor back' facies described by Scott 09).

TABLE VI

Relationship between infestation and the condition of haddock.

Size of haddock	Infestation	No. of fish examined	Average condition factor	Mean length cm	Mean weight g	% under- or over- weight
25-30 cm	No infestation	95	0·889	27·9	193	(100·0)
	Immature parasites	13	0·903	28·5	209	+8·3
	One mature parasite	34	0·826	27·6	174	−9·9
	Two mature parasites	5	0·772	28·1	171	−11·4
30-35 cm	No infestation	61	0·931	32·0	305	(100·0)
	Immature parasites	11	0·946	32·3	319	+4·6
	One mature parasite	23	0·833	32·2	278	−8·9
	Two mature parasites	6	0·615	32·8	217	−28·9

ANGES IN GROWTH

The only previous work concerning the retardation of growth due to the infestation with *Lernaeocera* hat by Desbrosses (1948), who examined that problem in whiting infested in *L. branchialis*. He found t the proportions of the body of infested whiting differed from those of the normal. The infested fish l a shallower body and its head was longer in relation to the total body length. The ratio was cal- ated according to the formula $\frac{100\ lt}{x}$ where 'lt' is the length of the head and 'x' total body length. e ratios were as follows: for the uninfested fish 24·5, for the infested fish 25·7. Desbrosses did not try explain this phenomenon, but it must be taken as implying that the head of the fish was relatively ger due to the differential retardation of the growth of the body rather than due to the increase in rate of growth of the head.

No such effects could be observed on haddock. A sample of 267 haddock has been examined in a ilar way and the ratios are the same for both groups of fishes. The relationship between the total gth of the body and infestation of the fish has also been examined. The results can be seen in Table VII. retardation of growth is noticeable. On the contrary, it appears from the table that in some cases average infested fish are larger than the uninfested fish of the same group. This paradoxical phenom- n is recorded by Sproston and Hartley (1941). They put forward an explanation (which they eventu- reject) that it must be due to the selective infestation of larger fishes. While this explanation merits re attention than it has so far received, especially in view of the general increase in the incidence of station with the growth and age of the fish, as described earlier in this paper, the available data allow

TABLE VII

Average sizes of infested and uninfested haddock.

Sample no.		2 years old		3 years old		4 years old		5 years old		6 years old		7 years old	
		No. fish	Mean length	No. fish	Mean length	No. fish	Mean length	No. fish	Mean length	No. fish	Mean length	No. fish	Mean length
1	NL	108	31·5	145	38·5	70	40·9	40	42·7	32	43·9	26	45·6
	L	20	33·9	54	37·9	23	41·9	8	41·5	4	43·0	13	47·1
2	NL	129	30·5	40	37·1	5	42·4						
	L	36	30·8	55	37·4	10	41·2						
3	NL	146	28·6	34	32·3								
	L	62	28·4	19	32·9								
4	NL	15	40·7	19	42·9	39	44·8	16	45·6	5	53·6		
	L	5	39·7	7	44·4	23	46·1	8	46·0	1	47·1		

NL—uninfested, L—infested. All the infested fishes carried fully developed adult parasites.

one to add very little to it. Statistical analysis shows no significant differences between the sizes of infe and uninfested fishes of each group.

Sexual development

This aspect of parasitic influence on haddock has not been extensively studied. A compariso the weights of the gonads of infested and uninfested fishes was made on a sample of 116 fishes, all years old and ranging in length between 24-33 cm. The fishes were all caught in the same locality at the same time. The following figures were obtained:

Males:	Uninfested	–	–	–	1·91 g
	Infested	–	–	–	1·22 g
Females:	Uninfested	–	–	–	1·10 g
	Infested	–	–	–	0·81 g

These values seem to indicate that parasitisation results in retardation of the growth of the gonads, gonads appearing to be more affected than females. The average values for the gonad weight rem consistently lower for the infested fishes even when the fish are divided into three cm length gro However, our knowledge of the normal conditions obtaining in haddock in this respect is far from per and all data must be interpreted with caution. The range of gonad weight of fishes of the same siz tremendous (one might be eight or ten times heavier than the other) and the ranges for the infested uninfested fishes show a great degree of overlap. All that can safely be said is that these figures give indication of the possibility of parasitic influence on the development of the gonads and show the which should be taken in future studies.

DISCUSSION

In all discussions of the effects of infestation of haddock with *L. obtusa* we must clearly disting two different ways in which this parasite harms its host. The first is the infliction of mechanical in to the tissues caused by the attachment of the parasite and the penetration of its head into the m blood vessels. This injury is of purely local character and is probably of little significance to the unless it results in the derangement of the circulation or unless it facilitates entry of pathogenic organi and infection. So far as is known, these effects are unusual, and on the whole the mechanical activiti the parasite can be regarded as having a small effect on the host.

The second and the most important part of the parasite's activity is its feeding, resulting in w drawal of relatively large quantities of the blood of the host. A direct result of this loss is second

naemia, the degree of which depends on the state of development of the parasite and the duration of its ctivity, as well as the number of the parasites on the individual host. All the deflections from the normal ı the host fish can be regarded as resulting from anaemia. In fact, all those deflections appear to form 'clinical picture' of untreated secondary anaemia. They include some loss of weight and general lassi- ıde, but no retardation of growth and development. If we compare the changes in the haddock with ıose caused by anaemia in man (taking children as an example, since they and the fish are actively owing) we find a considerable degree of analogy (Sheldon, 1946).

All the changes occurring in the infested fish show an amazing degree of parallelism (Fig. 8). The loss haemoglobin, the loss of liver fat and of weight can be tentatively explained as follows: the first drain ı the blood of the host acts as a stimulant. Haemopoietic organs are stimulated to produce more blood ıd the stimulation results in the haemoglobin level becoming higher than normal. With the rise in aemoglobin content rises also the oxygen uptake of the fish. The rate of oxygen uptake is closely related the metabolic rate of the animal and it might be followed by an increase in the activity and the con- quent increase in the food intake. This in turn might be followed by the increase of the fat content of e liver and perhaps some tendency to put on weight which, at any rate, shows no sign of decreasing r a period of several months. (An additional or even perhaps the main stimulant might be something the nature of a metabolite or secretion of the parasite, injected into the blood-strem of the host. Some cape of such substances is quite likely in view of the sucking action of the parasite's mouth and the versible peristalsis). As the feeding activity of the parasite becomes more vigorous, the drain continues ıd increases in severity until the response to stimulation can no longer maintain the normal state of the ıimal and the drop in haemoglobin content, with all the associated phenomena, is inevitable.

While few difficulties exist in understanding the fluctuations of the haemoglobin content, the same nnot be said about the other changes, for example the liver fat fluctuations. Even if the mechanism ggested above is accepted, it is quite clear that fluctuations in the fat content of the liver require far ore time than those of the haemoglobin content and that a period of the order of several weeks at ast might be necessary. As these changes are related to the development of the parasite it might be ferred that the young substages of the adult parasite must be of considerable duration. In fact, the aks of abundance of different substages in Fig. 2 imply that the period of attaining the reproductive ıge is about six months from the moment of attachment (page 7). This period should be quite sufficient r the fish to undergo any of the above-described changes. Thus it appears that the duration of the early bstages of the adult parasite, and the changes occurring in the host, support each other.

In giving an opinion on the effects of *L. obtusa* on its host, we must remember that they have been sessed in this paper in terms of average fish and that on many occasions infested haddock were found owing little or no discernible effects of infestation. The life span of the parasite on the final host is ly about $1\frac{1}{2}$ years and it has been observed that after that period, if no re-infestation follows, the fish able to recover and its condition returns to normal. All this prompts the opinion that the effects of *obtusa*, although definitely harmful and of some commercial interest (due to the loss of weight of the fested fishes and possibly due to influence on their fertility), are by no means directly fatal in themselves.

The author wishes to express his gratitude to all the members of the staff of the Marine Laboratory, berdeen, who assisted him in collection of data aboard the research vessels and in the Fish Market. s special thanks are due to Dr. B. B. Rae, Dr. J. H. Fraser and Mr. B. B. Parrish, whose interest, ticism and suggestions were of great value in writing this paper.

SUMMARY

The first part of this paper deals with the biology of *L. obtusa*. The life history of this copepod parasite haddock is discussed. By an examination of the relative abundance of various developmental phases roughout the year and by the age composition of the parasite population on the final host, its life ın is estimated as being about $1\frac{1}{2}$ years.

Reproductive activity and sexual behaviour of larvae have been observed by examining larval pulations on the intermediate host, the lemon sole. The period spent by the larvae on this fish has been

estimated at about six weeks. The maximum infestation period for lemon sole is April-May, that haddock is June-July. The minimum infestation period for haddock is in the spring, about March.

The distribution of the parasite is discussed and its dependence on the distribution and abunda of the hosts considered. The relationship between the abundance of lemon sole and the degree of festation of haddock is demonstrated. The rate of infestation increases with the size of the hadd The parasite attaches itself mainly in the postero-lateral corner of the gills and from there penetr the wall of a major blood vessel, from which, intermittently, it extracts blood, its sole food.

The second part of the paper is concerned with the effects of the parasite on the haddock. T effects consist of secondary anaemia with associated phenomena, loss of weight and loss of liver fat. three factors undergo increase initially, but then show marked decreases. The increase is prob caused by an overshooting of a compensatory reaction. No retardation of growth is observed. The p bility of a retardation of sexual development is suggested, but cannot be regarded as proved.

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